

ARCTODIAPTOMUS NOVOSIBIRICUS KIEFER, 1971
IN ALASKA AND NORTHWEST TERRITORIES,
WITH NOTES ON *A. ARAPAHOENSIS* (DODDS, 1915)
AND A KEY TO NEW WORLD SPECIES OF
ARCTODIAPTOMUS (COPEPODA: CALANOIDA)

Edward B. Reed

Abstract.—Diaptomid copepods identified in North American literature as *Diaptomus bacillifer* Koelbel, 1885 lack the prominent process on the posterior surface of the second article of the exopodite of the male right fifth leg, which is recognized as a hallmark of *A. bacillifer* and its immediate allies. Of the currently recognized species of *Arctodiaptomus*, the so-called *bacillifer* most clearly resembles *A. novosibiricus* Kiefer, 1971 and may be that species. If so then *A. novosibiricus* is known from the New Siberian Islands, St. Paul Island, St. Matthew Island and the northern coast of Alaska; Victoria Island, Bernard Harbour and Adelaide Peninsula, N.W.T. Ecological circumstances suggest that future collecting may fill in gaps in the present discontinuous distribution. *A. arapahoensis* (Dodds, 1915) bears a great morphological similarity to *A. acutilobatus* (G. O. Sars, 1903). Presently *A. acutilobatus* is known from the Altai mountains, Caucasus and Kurdistan mountains. *A. arapahoensis* is known in the Rocky Mountains of Colorado, Montana, British Columbia and Alberta. Future collecting seems unlikely to erase the present discontinuous distribution; therefore it seems advisable to retain both names.

The best-conceived, best-illustrated and most complete keys for the identification of North American freshwater copepods are contained in the 2nd Edition of Ward & Whipple's *Freshwater Biology* (Edmondson 1959) (Reid 1990).

Keys become dated not only through the discovery of "new" species but through studies of "old" species that lead to new insights and corrections in nomenclature, presumed affiliations and distribution. Not infrequently the identity of the species remains fairly constant, while its presumed affiliation at the genus level undergoes one or more revisions.

Ideally keys would fulfill two functions: identification in a systematic manner and express phylogenetic relationships (Gurney 1931). For reasons discussed by Gurney,

methodical routes to identification rarely satisfy the second function. One approach to methodical treatment is to reduce large and seemingly intractable groups to smaller, more manageable subgroups.

The genus *Diaptomus* Westwood, 1836 in the broad sense surely qualifies as a large group; Dussart & Defaye (1983) listed 406 species plus 15 incertae sedis and several subspecies. Kiefer (1932a, 1932b) attempted to find morphological groupings among the many named species of *Diaptomus*; in the latter paper he established a new subfamily, Diaptominae, in the family Diaptomidae G. O. Sars, 1903. In the Diaptominae, Kiefer place the genera *Diaptomus* Westwood, 1836, *Hemidiaptomus* G. O. Sars, 1903 and 10 new genera. In general non-North American copepodologists have

accepted Kiefer's genera. Students of North American diaptomids, especially those making comprehensive or intensive regional investigations, have been inclined to view Kiefer's genera as subgenera of *Diaptomus* Westwood, 1836; for example, Light (1939), Wilson (1959), Smith & Fernando (1978a) and Williamson (1991). However many others including Torke (1979) and Boileau & Hebert (1988) have accepted Kiefer's genera. Light (1939) noted that while many species possessed definite specific characters, the range of morphological variation within the genus was not great.

Wilson (1959) noted that the genera proposed by Kiefer lack the morphological gaps characteristic of other calanoid genera and added that more precise diagnoses, evaluation and interpretation of variation and distribution of North American species are required before formally defining genera.

Sadly we are no nearer today to a comprehensive taxonomic treatment of North American diaptomids than we were in 1959. Part of the difficulty may be in deciding on what constitutes a genus gap; a second less obvious difficulty may be in attempting to assess ecological niches in anthropocentric rather than copepodocentric terms.

Fewer additions and corrections have occurred among the North American Calanoida since 1959 than among the Cyclopoida or Harpacticoida (Reid 1990). However there are reasons to reexamine the status of two diaptomids appearing in Wilson's 1959 key: *Diaptomus bacillifer* Koelbel, 1885 and *D. arapahoensis* Dodds, 1915.

I use Kiefer's *Arctodiaptomus* genus because the arctodiaptomids possess a set of morphological characters none of which alone is sufficient to constitute a gap but in concert they produce a fairly coherent morphological, if confusing ecological grouping.

Specimens were dissected and examined in glycerin or lactic acid. Insofar as possible, examinations and drawings were made without cover slips. Details were verified with oil immersion lenses.

Marsh (1920) identified as *Diaptomus bacillifer* Koelbel, 1885 some copepods collected 6 October 1915 from a pond one foot in depth on a ridge 100 feet above sea level at Bernard Harbour, N.W.T. (68°45'N, 114°44'W). Concerning these animals Marsh wrote (1920 p. 6j): "Up to the present time no species of *Diaptomus* found on the American continent has been considered identical with those of Europe or Asia. Therefore a good deal of care was used to make certain that the identification of this species was correct. The determination is based on the original description of Koelbel, 1884 (sic), supplanted by the later descriptions, especially those of Sars and Schmeil."

In the same paper, Marsh said that he had examined specimens of *D. bacillifer* from Saint Paul Island, Alaska (57°07'N, 170°17'W).

Marsh (1924) synonymized *Diaptomus arapahoensis* Dodds, 1915 with *D. bacillifer* Koelbel, 1885. Marsh (1929) reaffirmed this synonymy with the words "an examination of the description reveals that *D. arapahoensis* is *D. bacillifer*."

Wilson (1953) stated that she had examined Marsh's specimens of *D. bacillifer* and found his identification to be correct. She, however, believed *D. arapahoensis* not to be conspecific with *D. bacillifer*, and treated them as two species (Wilson 1959).

Reed (1962, 1963) followed the lead of Marsh and Wilson and identified arctodiaptomids from Alaska and N.W.T. as *Diaptomus bacillifer*.

In 1956 while the late Mrs. Wilson was gathering specimens for a long-planned monograph on North American diaptomids (Damkaer 1988), I had the good fortune to work with her at the University of Saskatchewan for a short time. Wilson was completely aware that some European copepodologists were questioning Marsh's (1920) records of *Diaptomus bacillifer*. First, the press of larger, more demanding taxonomic problems, then ill health which cut short the proposed monograph (Damkaer 1988) pre-

vented Wilson from fully dealing with questions surrounding the identity of North American *D. bacillifer*.

Kiefer (1971) provided a complete review of taxonomy of the Arctodiaptomi; it is necessary here to recount only the portions which impinge directly on North American forms.

In 1885 Koelbel described and named *Diaptomus bacillifer* from specimens collected in Plattensee, Hungary. Also in that year Imhoff named *Diaptomus alpinus* from an alpine lake in Berner Oberland (Kiefer 1971).

Schmeil (1893) noted only one absolute difference between *bacillifer* and *alpinus*, the presence of a "Cuticularvorsprung am zweiten Aussenastsegment des rechten männlichen Greiffusses" of *D. bacillifer* (Kiefer 1971 p. 127). Schmeil did not believe that the "Cuticularvorsprung" was sufficient to differentiate *alpinus* and *bacillifer* as species and synonymized *alpinus* with *bacillifer*, thus placing his not inconsiderable prestige behind Koelbel's species.

Schmeil's decision had far-reaching effects. For more than the next half century the works of many prominent copepodologists would show the influence of Schmeil, including Giesbrecht and Schmeil (1898), Sars (1898, 1903b), Marsh in several papers, Damian-Georgescu (1966) and Dusart (1967) among others.

Kiefer (1932b) placed *D. bacillifer* in one of his new genera, *Arctodiaptomus*, and perhaps under the influence of Schmeil and others, omitted mention of *D. alpinus*. By the late 1960's the nomenclature of *Arctodiaptomus* had become so confused, particularly in regard to *bacillifer* and *alpinus*, that Kiefer (1971) undertook a revision of the genus.

Arctodiaptomus novosibiricus Kiefer, 1971
Fig. 1

Specimens examined.—Northwest Territories.—Victoria Island: Lady Franklin Point, 22 Aug 1957, Cambridge Bay

(69°03'N 104°05'W) 3 tundra ponds, 16 & 17 Sep 1957; Bernard Harbour: (68°44'N 114°27'W) little tundra pond, 20 Aug 1957; Adelaide Peninsula: shallow lake, 3 Sep 1957 (68°09'N 97°45'W). Alaska.—Near junction of Kikiakrorak and Colville rivers: (70°01'N 151°36'W), small tundra pond, 4 Aug 1955; Oliktok Point: (70°32'N 150°30'W), 3 tundra ponds, 24 & 25 Aug 1955; Point Barrow: (71°33'N 156°30'W), 3 tundra ponds, several dates 1963–64; Saint Matthews Island: (60°30'N 172°45'W), tundra ponds.

Description.—Most of the following description is based on Point Barrow specimens and checked against specimens from other localities.

Length without caudal setae: Most females ranged between 1.4 and 1.6 mm, one female from Adelaide Peninsula measured 1.8 mm. Males ranged between 1.2 and 1.45 mm.

Female: Body widest at mid-prosome (Fig. 1a). Pedigers 4 and 5 not divided dorsally, laterally a small furrow marks their joining (Fig. 1b). Posterior lateral margins pediger 5 moderately produced with lateral and dorsal sensilla. Genital segment little widened anteriorly, nearly symmetrical, lateral processes small, left with oblique postero-laterally directed sensillum, that of right projecting laterally (Fig. 1a), genital segment nearly as long as 2 succeeding segments and ramus combined. Urosome 2-segmented. Caudal rami about twice as long as wide, hairs on medial and lateral margins. Antennule extending to mid-genital segment (Fig. 1a); with 2 setae on articles 11 and 13, 1 on articles 14–19, seta on article 1 long, reaching beyond distal margin of article 5 (Fig. 1c). Rostrum small, pointed (ca. 25 μ m) (Fig. 1d). Lappet (Schmeil's organ) present on posterior surface of second article of endopodite leg 2 (Fig. 1e). Leg 5: posteriorly basipodite 1 extending over proximal end of basipodite 2; basipodite 2 with lateral seta near distal margin (Fig. 1f); exopodite 1 about 2.5 to 3 times longer than wide; exopodite 2 seta well developed, claw with

spinules on outer margin; exopodite 3, separated, setae strong, inner about twice as long as outer, endopodite of 2 articles, but dividing suture not always distinct, terminating in truncate margin, no setae, subapical row of hairs (Fig. 1f).

Male: Smaller, body shape similar to female. Rostral points short (ca. 25 μm), rounded, usual protrusion on right margin (Fig. 1g). Antennule: left similar to female in setation, except seta on article 1 short. Right antennule short spine on article 8, moderately long slender spines on articles 10 and 11, very small spine on article 12, short heavy spine on article 13 (Fig. 1h), seta on article 12 occasionally spine-like (Fig. 1i). Process of antepenultimate article long, straight, tip often slightly thickened (Fig. 1j), extending at least to mid-length of ultimate article. Lappet of leg 2 similar to that of female but smaller. Leg 5 left; basipodite 1 lacks process but may overhang proximal margin of basipodite 2 (Fig. 1k); basipodite 2 inner margin with thin, flexible, cuticular process (Fig. 1k) extending from mid-segment to mid-exopodite 1; exopodite terminal article with long, blunt fingerform outer process and curved, sharply pointed spine-like inner seta with spinules; proximal pad relatively small, hairy (Fig. 1l), endopodite 1- or 2-segmented, rounded, blunt tip, about equal to exopodite 1 in length, few small hairs. Leg 5 right: basipodite 1 with prominent process and sensillum (Fig. 1k, 1m) basipodite 2 with prominent semi-circular or elongate oval process on posterior surface (Fig. 1m), rounded process on proximal inner margin; flap-like cuticular membrane extending along middle $\frac{1}{3}$ to $\frac{1}{2}$ of inner margin; exopodite 1 projecting distally over exopodite 2 at outer margin, small prominences on posterior distal margin; exopodite 2 about twice as long as wide; lateral spine straight, about 1.3 times article width, inserted at distal $\frac{1}{4}$ of article, usually small cuticular process near base of spine; claw long, slender, recurved near tip. Endopodite 1- or 2-segmented, widened and rounded

on outer proximal margin, terminating in rounded and slanted tip bearing a sharp point on inner margin (Fig. 1n).

The Point Barrow specimens belong to the genus *Arctodiaptomus* as characterized in the key of Kiefer (1978) on the basis of these morphological features: 1) configuration of the terminal processes of the exopodite of male left fifth leg, 2) endopodite of female leg 5 armed only with a row of hairs, 3) two setae on article 11 of female and male left antennules and 4) spine of article 13 male right antennule not enlarged, spines of articles 10 and 11 strong, process of antepenultimate article straight.

Comparison. — Inexplicably, Marsh (1920) overlooked the prominent process on the posterior surface of basipodite article 2 of the male right fifth leg exopodite. This process is clearly visible in lateral view of the intact specimen (Fig. 1m). Cover slip pressure on a dissected leg five may cause the protrusion of basipodite article 1 to flatten, obscuring the process of article 2.

Marsh's (1920) description and drawings do not mention or show a cuticular process on the second segment of the male right exopodite leg five. Notes in the Marsh Collection at the National Museum of Natural History, Smithsonian Institution reveal that Marsh compared descriptions and drawings of several authors in regard to this process. Perhaps the most telling is this note in respect to the Canadian Arctic Expedition specimens: "Differs from Giesbrecht's analysis only in 2nd seg rt exop having no [cuticular-vorsprung]." Since Schmeil had already accepted the presence or absence of the "Vorsprung" as less than specific value, Marsh did not think it worth mentioning in his account of North American *bacillifer*.

The Point Barrow males resemble males of *A. alpinus* in lacking a process on the posterior surface of the right second exopodite article, but differ in minor respects of the right antennule.

The Point Barrow females are similar to some other arctodiaptomid females in se-

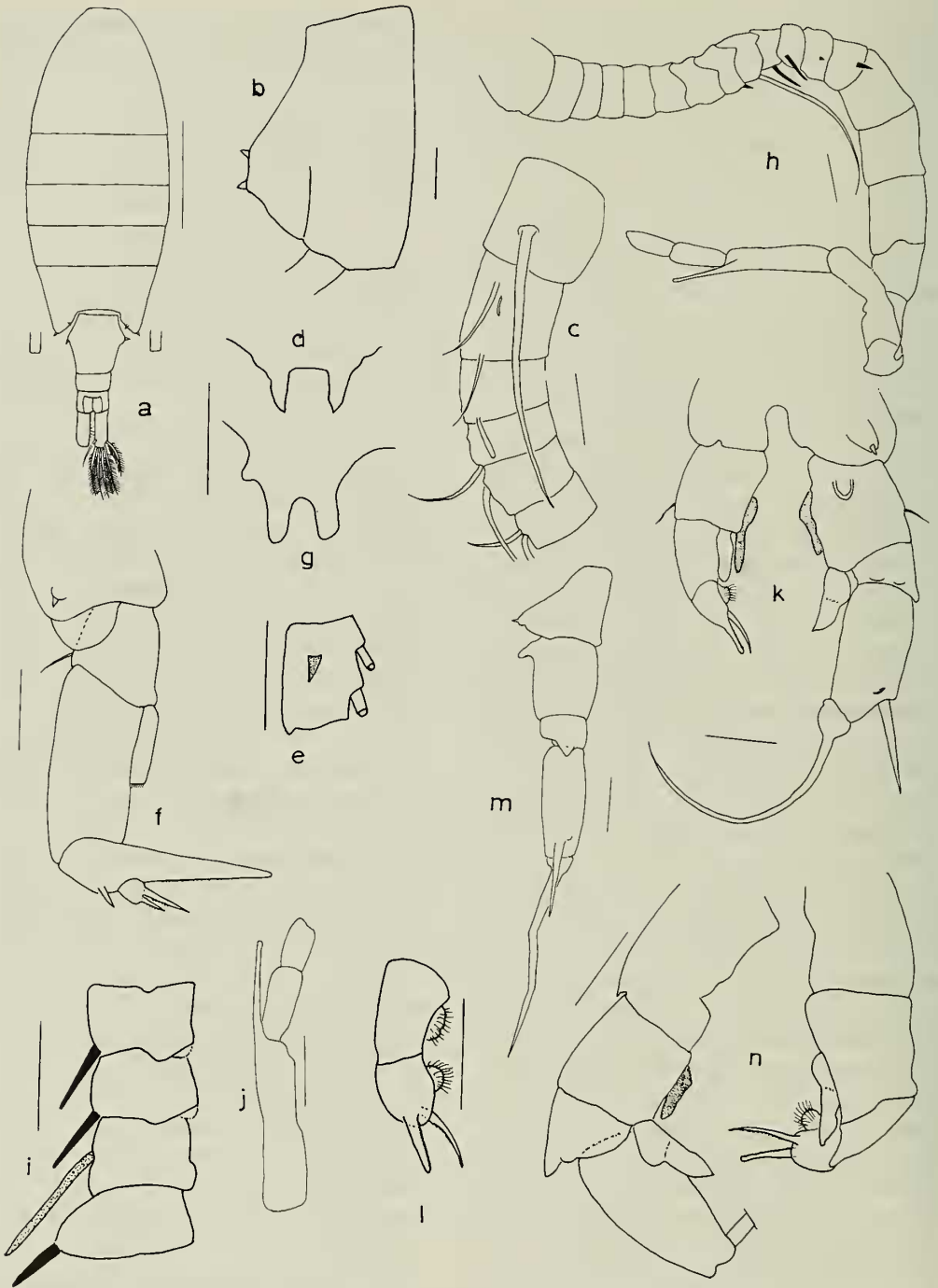


Fig. 1. *Arctodiaptomus novosibiricus*. Female: a, habitus; b, pedigers 4 and 5, lateral view; c, antennule articles 1-6; d, rostrum; e, Schmeil's organ; f, leg 5. Male: g, rostrum; h, right antennule; i, spines on right antennule articles 10-13; j, last three articles, right antennule; k, fifth legs, posterior view; l, exopodite left leg 5; m, right exopodite, lateral view; n, fifth legs, anterior view. Scale: a, 400 μ m, all other bars 50 μ m.

Table 1.—Subgeneric classification (A, H, R) number of setae () on articles 11, 13, 15 of female and male left antennule and presence (+) or absence (–) of process on posterior surface of 2nd article, right exopodite, male leg 5 of some *Arctodiaptomus* species. Data from Kiefer (1971).

11 (1)	11 (2)	11 (2), 13 (2)	11 (2), 13 (2), 15 (2)
<i>kurilensis</i> Kiefer, 1937 H +	<i>byzantinus</i> (Mann, 1940) A –	<i>alpinus</i> (Imhoff, 1885) R –	<i>acutilobatus</i> (G. O. Sars, 1903) R
<i>parvispineus</i> Kiefer, 1935 H ?	<i>burduricus</i> Kiefer, 1939 R –	<i>bacillifer</i> (Koelbel, 1885) R +	<i>centetes</i> (Brehm, 1938) R +
<i>nepalensis</i> Ueno, 1966 H ?	<i>dentifer</i> (Smirnov, 1928) A + <i>dudichi</i> (Kiefer, 1932) A –	<i>laticeps</i> (G. O. Sars, 1863) A – <i>niethammeri</i> (Mann, 1940) R –	<i>similis</i> (Baird, 1859) A + <i>arapahoensis</i> (Dodds, 1915) R
<i>saltillinus</i> (Brewer, 1898) (A) +	<i>kerkyrensis</i> (Pesta, 1935) A +	<i>novosibiricus</i> Kiefer, 1971 R –	
<i>floridanus</i> (Marsh, 1926) (A) +	<i>pectinicornis</i> (Wierzejski, 1887) A –	<i>piliger</i> (Brehm, 1955) A –	
<i>dorsalis</i> (Marsh, 1907) (A) +	<i>salinus</i> (Daday, 1885) R –	<i>osmanus</i> Kiefer, 1974 A ?	
<i>asymmetricus</i> (Marsh, 1907) (A) +	<i>spinus</i> (Daday, 1891) R – <i>steindachneri</i> (Richard, 1897) A + <i>stephanidesi</i> (Pesta, 1935) A – <i>wierzejski</i> (Richard, 1885) A – <i>arapahoensis</i> (Dodds, 1915) R + <i>acutilobatus</i> (G. O. Sars, 1903) R +		

Subgenera: A, *Arctodiaptomus* s. str.; H, *Haplodiaptomus*; R, *Rhabdodiaptomus*.

tation of articles 11 and 13 (Table 1) and in possessing a lateral furrow between the fourth and fifth thoracic segments. The rostrum of female *bacillifer* is long (40–50 μm); whereas those of *alpinus*, *laticeps* and *novosibiricus* are short (20–25 μm).

Sars (1898) identified the New Siberian diaptomids as *D. bacillifer* Koelbel. Sars' description of the New Siberian specimens is sketchy but his figures clearly show no process on the posterior surface of the second article of the male right fifth leg. Sars (1898:332) stated: "This (*D. bacillifer*) is one of the most characteristic Copepoda of the territory, occurring in great abundance as far north as the Expedition has reached." Sars also stated (1898:333): "This species is also recorded by Prof. Lilljeborg from Nor-

denskjolds Expedition, as occurring at In-serowa on the Siberian continent." In the synonymy of *D. bacillifer*, Sars listed "*D. retusus*, Lilljeb. Ms." Perhaps Lilljeborg's *D. retusus* name was never published; neither Kiefer (1971, 1978) nor Dussart and Defaye (1983) mention a *D. retusus*.

The lack of the process on the posterior surface of article 2, male right exopodite fifth leg led Kiefer (1971) to reject Sars' identification as *D. bacillifer* for the New Siberian specimens. He placed them in the *A. alpinus* group and named them *A. novosibiricus*. Apparently no specimens of *novosibiricus* from Siberia have come to hand since Sars' (1898) collections. Borutskyi et al. (1991) in their review of freshwater calanoids of U.S.S.R. and discussion of *A. no-*

vosibiricus list only the island of Lachovski, one of the New Siberian Islands from whence Sars' specimens came.

The couplet which distinguishes male *novosibiricus* from male *alpinus* in Kiefer's (1971) key reads:

Seitendorn des 2 Aussenastgliedes
rechts insertiert nahe der Basis der
Endklaue (Abb. 41); Fortsatz des
drittletzten Gliedes des Greifan-
tenne sehr lang und zugespitzt (Abb.
41) *novosibiricus*
Seitendorn sitzt etwa im 2 Drittel
des Aussenrandes (Abb. 28–30);
Fortsatz des drittletzten Gliedes der
Greifantenne wie (Abb. 16a, 22, 25,
26, 28–30, 37–39) *alpinus*

The females of *A. alpinus* and *A. novosibiricus* fall out together in Kiefer's (1971) key.

In Kiefer's (1978) key males of *A. novosibiricus* are separated from males of *A. alpinus* by the length of the process on the antepenultimate article of the right antennule: that of *alpinus* being at most as long as the following segment or usually shorter and that of *novosibiricus* at least as long as the following segment or much longer.

Again in the key to females, *alpinus* and *novosibiricus* fall out together along with *A. laticeps*. Male *A. laticeps* are quite different from males of *novosibiricus* and *alpinus* in several characters.

If one accepts Kiefer's (1971) revision of the Arctodiaptomi, then the lack of a process on the posterior surface of the second article of the male fifth right exopodite is a strong argument to reject Marsh's designation of *D. bacillifer* for the Canadian Arctic Expedition specimens and by extension for the present animals. The morphological differences between *alpinus* and *novosibiricus* are not great and ultimately they may be shown to be conspecific. For the time being the least objectionable course is to designate the North American form as *A. novosibiricus* Kiefer, 1971, partly on morphological

evidence and partly on distributional and ecological considerations.

Sars (1898) provided no ecological data for *A. novosibiricus* collected on the New Siberian Islands. In North America, *A. novosibiricus* is an inhabitant of small and shallow ponds. The Point Barrow specimens came from tundra ponds less than 250 m² in area, that varied in depth through the summer from 15 to 51 cm (Kalff 1967). The Adelaide Peninsula pond was about 6 ha, but less than 1 m deep. A polygon pond containing *A. novosibiricus* at Kikiakroarak was about 40 m² in area and 10 cm in depth.

Arctodiaptomus arapahoensis

(Dodds, 1915)

Fig. 2

Specimens examined.—Colorado.—Larimer County: East (3295 m) and West Rainbow lakes, Rawah Wilderness Area; Jackson County: Lower Slide Lake; Hinsdale County: Emerald Lake (3112 m); San Juan County: Silverking, Ice (3752 m), Fuller (3843 m) lakes; Pitkin-Lake counties: alpine tundra ponds, Independence Pass (3689 m).

Description.—Most of the following description and drawings are based on East Rainbow and Silverking specimens and checked against specimens from other localities.

Female: Dodds (1915) gave the lengths of females that he examined as from 1.6 to 2.1 mm and lengths of males between 1.35 and 1.7 mm. Sixteen females from East Rainbow Lake ranged between 1.46 and 1.75 mm, mean 1.53; 28 males ranged between 1.32 and 1.48, mean 1.41 mm.

Wings of last prosome segment produced posteriorly past level of sensilla on genital segment (Fig. 2a). Reflexed antennules extend to midlength of genital segment, which is essentially symmetrical, about 1.1 times longer than greatest width, sensilla directed postero-laterally. Urosome segments 2 & 3 combined about equal to length of genital segment. Rami haired on inner margins.

Rostrum well developed, about 100 μm

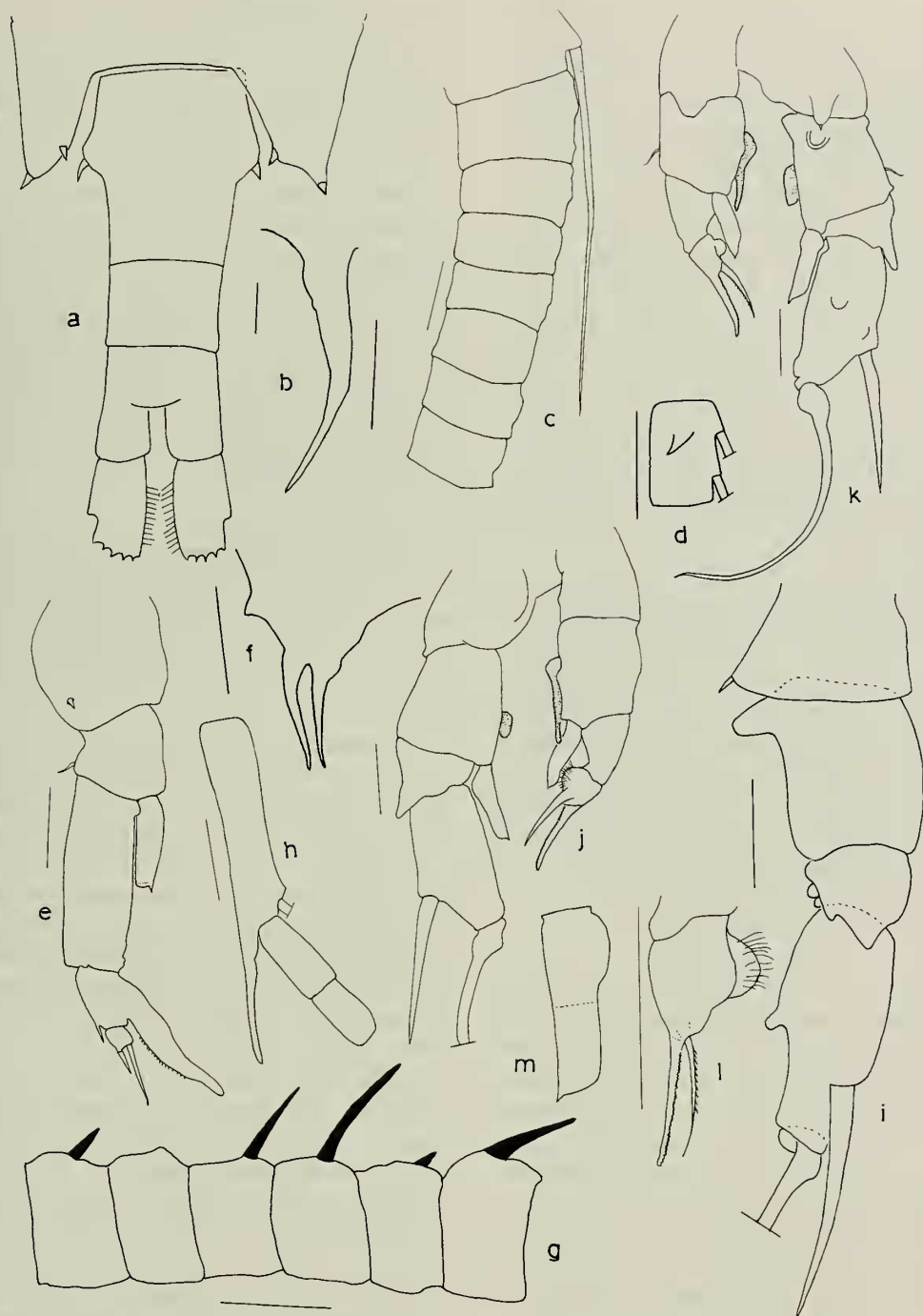


Fig. 2. *Arctodiaptomus arapahoensis*. Female: a, pediger 5 and urosome; b, rostrum; c, antennule segments 1-8; d, Schmeil's organ; e, leg 5. Male: f, rostrum; g, right antennule, spines on articles 8-13; h, last three articles, right antennule; i, right exopodite leg 5, lateral view; j, fifth legs, posterior view; k, fifth legs, anterior view; l, terminal articles, left exopodite; m, right endopodite. Scale: a, 400 μ m, all other bars 50 μ m.

in length (Fig. 2b). Seta of first segment of antennule about 260 μm long, extending to midlength of article 7 (Fig. 2c). Antennule articles 9, 11, 13 and 15 with 2 setae each.

Second article of endopodite leg 2 bearing hyaline lappet (Schmeil's organ) (Fig. 2d).

Leg 5. Basipodite 2 with small process bearing a short, moderately strong spine (Fig. 2e). Inner margin basipodite 2 much longer than outer margin. First article of exopodite long, slender, about 2 times as long as wide; claw of second article sinuous on inner margin, finely denticulate on outer. Article 3 of exopodite well developed, distinct from article 2, outer seta about twice the length of inner, both well developed and slightly spinulose. Endopodite of one article, end square bearing few hairs, with spine on inner corner.

Male: Rostrum smaller than that of female, tips 40 to 50 μm , right side with usual protuberance on margin (Fig. 2f). Left antennule articles 9 and 11 with 2 setae, one seta on articles 12–17. Right antennule, article 8 with short spine, spines of articles 10 and 11, moderately long, slender; spine of article 12 short, spine of article 13 moderate (Fig. 2g); antepenultimate article with long slender process extending nearly to distal end of last article (Fig. 2h).

Schmeil's organ smaller than that of female.

Right leg 5, basipodite article 1 with prominent posterior process; basipodite 2 with posteriorly directed process on posterior margin (Fig. 2i, k), flap of hyaline membrane mid-inner margin; exopodite article 1 produced into point on outer margin (Fig. 2i, k) exopodite article 2 with process on posterior face at midlength (Fig. 2i, k) small hyaline process near base of lateral spine; lateral spine stout, inserted at distal $\frac{1}{3}$ of article and about equalling or exceeding article length. Claw long, curved, slender, finely denticulate, with recurved tip. Endopodite long, nearly reaching midlength of exopodite 2, apex oblique, acute.

Left leg (Fig. 2j, k), basipodite 2 with long,

hyaline process on inner margin; digital process of terminal article of exopodite elongate, somewhat broadened, with roughened inner border (Fig. 2l); inner process a stout, spinulose spine (Fig. 2l). Endopodite 1 article, terminating in sharp tip.

Curiously Dodds (1915) failed to either mention or figure the prominent process on the posterior surface of the second basipodite of the exopodite of the right male fifth leg. *A. arapahoensis* bears an unmistakably clear morphological resemblance to *A. acutilobatus*, (G. O. Sars, 1903) (Sars 1903b). In 1953 when Wilson called attention to this resemblance, the setation of the antennules of *acutilobatus* was not known, and she believed more information was needed to decide conspecificity. Kiefer (1971) found the setation of *acutilobatus* to be exactly the same as that reported for *arapahoensis*, but perhaps for want of further information, took no stand on the conspecificity of *arapahoensis* and *acutilobatus*.

Arctodiaptomus arapahoensis is known from the Rocky Mountains of Colorado (Dodds 1915, Reed & Olive 1958, Wilson 1959), Montana (Wilson 1959) and British Columbia and Alberta (Anderson 1974). *Arctodiaptomus arapahoensis* has been most frequently found in lakes ranging from 1.4 to 150 ha and 2.5 to 34 m deep; however the Independence Pass record shows that it is capable of inhabiting smaller and shallower waters.

Kiefer (1971) listed *A. acutilobatus* from the Altai mountains, lakes and ponds in the Caucasus mountains from 1800 to 3200 m and the mountains of Kurdistan (Turkey). To these locations Kiefer (1978) added Mongolia and "Mundungsgebiet der Samara."

In spite of the morphological congruity of Colorado specimens with Kiefer's figures and descriptions of *A. acutilobatus*, it is my opinion that Dodd's name *arapahoensis* should be retained for the North American form on distributional considerations.

Discussion

The morphological similarity of *A. novosibiricus* to an arctodiaptomid occurring along the northern coast of North America and that of *A. acutilobatus* and *A. arapahoensis*, at least in the characters used, is unquestioned. In the understanding of present day biological species, morphological similarity or lack thereof is not a sure guide to conspecificity or species distinctness. In addition to external morphology, ecological, physiological, behavioral, and most of all, information on reproductive compatibility must be evaluated in answering questions concerning conspecificity. Breeding experiments, chromosomal studies, allozyme analyses, electrophoresis and other biochemical techniques have supported distinctness of species initially based on minor morphological differences (Boileau & Herbert 1988). In some instances of morphological differences, conspecificity has been established by chromosomal techniques (Einsle 1963). In still other instances reproductive isolation has been shown in species that could not be differentiated morphologically (Price 1958, Boileau 1991).

A decision regarding the designation of North American arctodiaptomids requires a presently unverifiable assumption regarding reproductive status. The data which would shed light on their standings as biological species are not available, nor are they likely to be available soon. A comparative study requiring live specimens would be useful. However, for practical reasons, the probability of such a study actually happening must be vanishingly small.

The North American populations of *A. arapahoensis* and Eastern Hemisphere populations of *A. acutilobatus* if reproductively isolated could represent two or more sibling species; if not reproductively isolated, then one species and possibly several subspecies.

We are still learning about gene flow between widely separated and nearby populations. *A. acutilobatus* and *A. arapahoensis*

seem to occur in mountainous areas that are separated from each other by broad steppes, prairies, deserts and a broad expanse of ocean. Future collecting will almost certainly increase the number of waters known to contain these species in their respective mountainous areas but seems unlikely to produce populations in the vast areas separating the mountainous regions. Allopatry on the scale shown by *acutilobatus* and *arapahoensis* generally hints at different species rather than discontinuous distribution of one species. Hence my opinion that both be retained as species pending information on reproductive compatibility.

It is not known if *A. novosibiricus* from the new Siberian Islands would in fact produce viable offspring with Point Barrow or Bernard Harbour copepods. The few ecological data available suggest that they may occupy similar habitats.

The Siberian coastal regions north of the tree line contain very numerous bodies of water which range greatly in extent and depth (Zhadin & Gerd 1961). Black & Barksdale (1949) estimated that areas on the Alaskan Coastal Plain are 20 to 90 percent covered by water. Holmquist (1975) emphasized not only the number of ponds and lakes along the North American northwestern coast, but also the diversity of ecological conditions in them. Because of the similarity of terrain along the Arctic coasts of Siberia and North America, future collecting of copepods seems likely to fill in spaces between the presently known populations, thus reducing the discontinuity of distribution, and the likelihood of reproductive isolation.

Kiefer's 1971 study clearly illustrated the overall great similarity of many *Arctodiaptomus* species and simultaneously illustrated variation in morphological characters and combinations of characters. His study also underlines the importance of examining both sexes before reaching conclusions about identity. Females that are virtually specifically indistinguishable may belong with

males that are clearly separable and *vice versa*.

In establishing subgenera of *Arctodiaptomus* Kiefer relied heavily on the form of the process of the third from last article of the male right antennule and on the 14th article of the antennule, as well as characters of the 5th pair of legs.

Which of the morphological characters are chosen for emphasis will greatly influence the species groupings within the *Arctodiaptomi*. Kiefer's emphasis on male right antennules led to grouping together forms which have quite different patterns of antennular setation. Grouping by antennular setation leads to mixing together species with other different morphological characters. At least four patterns of setation on the female antennules and male left antennule are known in the genus *Arctodiaptomus* (Table 1). The presence or absence of a process on the posterior surface of the second exopodite article of the male right leg 5 does not seem to bear a consistent relationship to antennular setation.

Key to New World species of *Arctodiaptomus*

- 1a. One seta on article 11 of ♂ left and both ♀ antennules 4
- 1b. Two setae on article 11 2
- 2a. Two setae on article 11, one seta 13-17
 ♂ *A. arapahoensis* (Dodds, 1915)
- 2b. Two setae on article 13, one or two on articles 13-17 3
- 3a. Two setae on 13, one on article 15
 *A. novosibiricus* Kiefer, 1971
- New Siberian Islands, Alaska, Northwest Territories
- 3b. Two setae on articles 13 and 15
 ♀ *A. arapahoensis* (Dodds, 1915)
- Colorado, Montana, British Columbia, Alberta
- 4a. Genital segment: ♀, right side produced into a large lateral lobe distal to usual process bearing sensil-

- lum. Leg 5 ♂ right exopodite 2, lateral spine thick, less than length of article
 *A. symmetricus* (Marsh, 1907)
- Cuba Marsh (1907)
- 4b. Genital segment ♀, large distal lobe lacking. Leg 5 ♂ exopodite 2, length of lateral spine about equal to or greater than that of article 5
- 5a. Leg 5 ♀, endopodite as long or nearly as long as exopodite 1, ♀ pediger 4, usually with single, double or triple medial dorsal process. Leg 5 ♂, right exopodite 2, lateral spine inserted proximal to mid-length of article, longer than article; left basipodite 2, width and length about equal
 *A. dorsalis* (Marsh, 1907)
- Arizona (Cole 1961), Louisiana (Marsh 1907), Mississippi (Harris 1978), Oklahoma (Robertson 1970), Cuba (Smith & Fernando 1978b), Haiti (Kiefer 1936) as *D. proximus*, Costa Rica (Collado et al. 1984), Mexico (Suárez 1991), Colombia (unpub. Suárez & Reid 1992), Nicaragua (Herbst 1960) as *D. alter*, Venezuela (González 1968) as *D. proximus*.
- 5b. Leg 5 ♀, endopodite 1/2 to 3/4 length of inner margin exopodite 1; ♀ pediger 4, with or without dorsal medial process. Leg 5 ♂, right exopodite 2 lateral spine inserted at mid-length or distally, spine length about equal to article length; left basipodite 2 longer than wide . . . 6
- 6a. Right metasomal wing ♀ produced outward beyond lateral margin of body (dorsal view). Leg 5 ♂, right exopodite greatly exceeding length of inner margin exopodite 1, lateral spine exopodite 2 inserted at mid-length of article. Right antennule ♂, antepenultimate article without process
 *A. kurilensis* Kiefer, 1937

- Kurile Islands (Kiefer 1937), Aleutian Islands (Wilson 1959)
- 6b. Right metasomal wing ♀ not protruding beyond lateral margin of body. Leg 5 ♂ right exopodite, lateral spine inserted near distal end of article; right endopodite little if any longer than inner margin of exopodite 1. Right antennule ♂, antepenultimate article with curved distal process 7
- 7a. Caudal ramus ♀, usually with hairs on inner margin only, pediger 4 with or without dorsal medial process. Leg 5 ♀, claw of exopodite 2 about as long as exopodite 1. Leg 5 ♂, basipodite 2 with small hyaline process on inner margin
. *A. saltillinus* (Brewer, 1898)
- Nebraska (Brewer 1898), Oklahoma (Robertson 1970), Texas (Wilson 1953).
- 7b. Caudal ramus ♀, Usually with hairs on inner and outer margins. ♀ pediger 4 with or without dorsal medial process. Leg 5 ♀, claw of exopodite 2 much shorter than exopodite 1. Leg 5 ♂, basipodite 2 lacking inner hyaline process
. *A. floridanus* (Marsh, 1926)
- Florida (Marsh 1926), Georgia (Humes 1950) as *D. albuquerquensis* det. by Wilson (1953), Oklahoma (questionable record by Keeton 1959); discussed by Robertson (1970).

Acknowledgments

I am indebted to the following people for the use of specimens of *A. novosibiricus* from Alaska and Northwest Territories: J. Kalf, Alaska; J. Bond, Bernard Harbour and Victoria Island; E. and A. MacPherson, Adelaide Peninsula. W. C. Nelson loaned specimens of *A. arapahoensis* from Colorado lakes.

I thank Janet W. Reid for providing cop-

ies of literature from the Wilson Copepod Library and Marsh's notes concerning specimens from the Canadian Arctic Expedition. I am particularly indebted to Janet W. Reid for aid in developing the key to New World arctodiaptomids and to her and M. F. Suárez for permission to use their unpublished record of *A. dorsalis* from Colombia.

Thomas Bowman kindly offered many helpful comments on an early draft manuscript. Two anonymous reviewers provided helpful comments.

Literature Cited

- Anderson, R. S. 1974. Crustacean plankton communities of 340 lakes and ponds in and near the National Parks of the Canadian Rocky Mountains.—*Journal of the Fisheries Research Board of Canada* 31:855–869.
- Black, R. F., & W. L. Barksdale. 1949. Oriented lakes of northern Alaska.—*Journal of Geology* 57:105–118.
- Boileau, M. G. 1991. A genetic determination of cryptic species (Copepoda: Calanoida) and their postglacial biogeography in North America.—*Zoological Journal of the Linnean Society* 102: 375–396.
- , & P. D. N. Hebert. 1988. Electrophoretic characterization of two closely related species of *Leptodiaptomus*.—*Biochemical Systematics and Ecology* 16:329–332.
- Borutsky, E. V., L. A. Stepanova, & M. S. Kos. 1991. Keys to the freshwater Calanoida of U.S.S.R. Zoological Institute, Russian Academy of Science, Saint Petersburg, 503 pp. (In Russian with English summary).
- Brewer, R. H. 1898. A study of the Copepoda found in the vicinity of Lincoln, Nebraska.—*Journal of the Cincinnati Society of Natural History* 19: 119–138.
- Cole, C. A. 1961. Some calanoid copepods from Arizona, with notes on congeneric occurrences of *Diaptomus* species.—*Limnology and Oceanography* 6:432–443.
- Collado, C., D. Defaye, B. H. Dussart, & C. H. Fernando. 1984. The freshwater Copepoda (Crustacea) of Costa Rica with notes on some species.—*Hydrobiologia* 199:89–99.
- Damian-Georgescu, A. 1966. Calanoida (forma de apă dulce). *In* Fauna Republicii Populare Române, Crustacea 4(8):1–130.
- Damkaer, D. M. 1988. Mildred Stratton Wilson, co-

- pepodologist (1909–1973).—*Journal of Crustacean Biology* 8:131–146.
- Dodds, G. S. 1915. Descriptions of two new species of Entomostraca from Colorado, with notes on other species.—*Proceedings of the United States National Museum* 49:97–102.
- Dussart, B. 1967. Les Copépodes des eaux continentales d'Europe occidentale, Volume I, Calanoides et Harpacticoides. N. Boubée et Cie, Paris.
- , & D. Defaye. 1983. Répertoire Mondial des Crustacés Copépodes des Eaux Intérieures. I. Calanoides. Centre National de la Recherche Scientifique, Paris.
- Edmondson, W. T. (ed.). 1959. *Freshwater biology*. 2nd ed. John Wiley & Sons, Inc., New York.
- Einsle, U. 1963. Untersuchungen über die Variabilität in *Cyclops furcifer* Claus, 1957.—*Crustaceana* 5:193–204.
- Giesbrecht, W., & O. Schmeil. 1898. Copepoda. I. Gymoplea. In *Das Tierreich* 6 Lieferung. Berlin. XIV + 169 pp.
- González, S. A. 1968. Desarrollo Larvario de *Diaptomus proximus* Kiefer (Copepoda, Calanoida).—*Hydrobiologia* 32(3–4):528–544.
- Gurney, R. 1931. *British fresh-water Copepoda*. Volume I, Ray Society, London.
- Harris, M. J. 1978. Copepoda of northern Mississippi with a description of a new subspecies.—*Tulane Studies in Zoology and Botany* 20(1–2):27–34.
- Herbst, H. V. 1960. Copepoden (Crustacea, Entomostraca) aus Nicaragua und Südperu.—*Gewässer und Abwässer* 27:27–54.
- Holmquist, C. 1975. Lakes of Northern Alaska and northwestern Canada and their invertebrate fauna.—*Zoologische Jahrbucher für Systematik* 102:333–484.
- Humes, A. G. 1950. Experimental copepod hosts of the broad tapeworm of man, *Dibothriocephalus latus* (L.).—*Journal of Parasitology* 36:541–547.
- Imhoff, O. E. 1885. Über die “blassen Kolben” und den vorderen Antennen der Süßwasser-Calaniden.—*Zoologischer Anzeiger* 8:353–356.
- Kalf, J. 1967. Phytoplankton abundance and primary production rates in two arctic ponds.—*Ecology* 48:558–565.
- Keeton, D. 1959. Limnological effects of introducing oil field brine in farm ponds to reduce the turbidity.—*Oklahoma Fishery Research Laboratory, Report 72*. (cited in Robertson, 1970).
- Kiefer, F. 1932a. Versuch eines Systems der altweltlichen Diaptomiden (Copepoda Calanoida).—*Zoologischer Anzeiger* 100(7/8):213–220.
- . 1932b. Versuch eines Systems der Diaptomiden (Copepoda Calanoida).—*Zoologische Jahrbucher, Abteilung für Systematik, Ökologie und Geographie der Tiere* 63:451–520.
- . 1936. Freilebende Süß- und Salzwassercopepoden von der Insel Haiti.—*Archiv für Hydrobiologie* 30:263–317.
- . 1937. Süßwassercopepoden aus Ostasien.—*Zoologischer Anzeiger* 118(11/12):299–301.
- . 1971. Revision der *bacillifer*-Gruppe der Gattung *Arctodiaptomus* Kiefer. (Crustacea Copepoda: Calanoida).—*Memorie dell'Istituto Italiano di Idrobiologia* 27:113–267.
- . 1978. Das Zooplankton der Binnengewässer 2. Teil Freilebende Copepoda.—*Die Binnengewässer* 26:1–343.
- Koelbel, C. 1885. Carcinologischer.—*Sitzungsberichte der Akademie von Wissenschaften Wien* 90:312–326.
- Light, S. F. 1939. New American subgenera of *Diaptomus* Westwood (Copepoda, Calanoida).—*Transactions of the American Microscopical Society* 58:473–484.
- Marsh, C. D. 1907. A revision of the North American species of *Diaptomus*.—*Transactions of the Wisconsin Academy of Science* 15:381–516.
- . 1920. Report of the Canadian Arctic Expedition 1913–18. Volume VII: Crustacea, Part J: Freshwater Copepoda, 1–25. J. de La-roquerie Tache. Ottawa.
- . 1924. A new locality for a species of *Diaptomus*.—*Science* 59:485–486.
- . 1926. On a collection of Copepoda from Florida with a description of *Diaptomus floridanus*, new species.—*Proceedings of the United States National Museum* 70, Article 10:1–4.
- . 1929. Distribution and key of the North American copepods of the genus *Diaptomus*, with the description of a new species.—*Proceedings of the United States National Museum* 75(14):1–27.
- Price, J. L. 1958. Cryptic speciation in the *vernalis* group of Cyclopoida.—*Canadian Journal of Zoology* 36:285–303.
- Reed, E. B. 1962. Freshwater plankton Crustacea of the Colville River area, northern Alaska.—*Arctic* 15:27–50.
- . 1963. Records of freshwater Crustacea from arctic and subarctic Canada. In *Contributions in Zoology*.—*Bulletin of the National Museum of Canada* 199:29–62.
- , & J. R. Olive. 1958. Altitudinal distribution of some entomostraca in Colorado.—*Ecology* 39:66–74.
- Reid, J. W. 1990. Taxonomic reference list for North American free-living Copepoda.—*Bulletin of the North American Benthological Society* 7:227–232.
- Robertson, A. 1970. Distribution of calanoid copepods (Calanoida, Copepoda) in Oklahoma.—*Proceedings of the Oklahoma Academy of Science* 50:98–103.

- Sars, G. O. 1898. The Cladocera, Copepoda and Ostracoda of the Jana Expedition.—*Annuaire du Muséum Zoologique de l'Académie Impériale des Sciences de St. Petersbourg* 3:324–359 + 6 plates.
- . 1903a. Copepoda Calanoida. An account of the Crustacea of Norway, with short descriptions and figures of all the species, 4:1–xiii 145–171, Bergen Museum, Bergen.
- . 1903b. On the crustacean fauna of Central Asia. Part III. Copepoda and Ostracoda.—*Annuaire de Muséum Zoologique de l'Académie Impériale des Sciences de St. Petersbourg* 8:196–232.
- Schmeil, O. 1893. Copepoden des Rhätikon-Gebirges.—*Abhandlungen Naturforschung Gesellschaft Halle* 19:1–40.
- Smith, K., & C. H. Fernando. 1978a. A guide to the freshwater calanoid and cyclopoid copepod Crustacea of Ontario. Department of Biology, University of Waterloo, Ontario, 74 pp.
- , & ———. 1978b. The freshwater calanoid and cyclopoid copepod Crustacea of Cuba.—*Canadian Journal of Zoology* 56:2015–2023.
- Suárez, E. 1991. Nuevo registro de *Diaptomus dorsalis* Marsh (Copepoda: Calanoida) en México y su distribución en la zona epicontinental central del Caribe Mexicano.—*Caribbean Journal of Science* 27:200–203. (In Spanish with English summary).
- Torke, B. G. 1979. Crustacean zooplankton data for 190 selected Wisconsin inland lakes.—Wisconsin Department of Natural Resources Research Report 101:1–69.
- Westwood, J. O. 1836. Art. Cyclops. Pp. 227–238 in C. F. Partington, ed., *The British cyclopaedia of natural history* Vol. II. London.
- Williamson, C. E. 1991. Copepoda Pp. 787–822 in J. Thorp & A. Covich, eds., *Ecology and classification of North American freshwater invertebrates*. Academic Press, Inc., San Diego.
- Wilson, M. S. 1953. New and inadequately known North American species of the copepod genus *Diaptomus*.—*Smithsonian Miscellaneous Collections* 122(2):1–30.
- . 1959. Calanoida. Pp. 738–794 in W. T. Edmondson, ed., *Fresh-water biology*. John Wiley & Sons, Inc., New York.
- Zhadin, V. I., & S. V. Gerd. 1961. Fauna and flora of the rivers, lakes and reservoirs of the U.S.S.R. State Training and Pedagogical Publishing House, Moscow, 599 pp. (In Russian, English Translation by Israel Program for Scientific Translations. Jerusalem, 626 pp. 1963).

1901 Stover Street, Fort Collins, Colorado 80525, U.S.A.